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THE LARVAL DEVELOPMENT AND METAMORPHOSIS OF THE PEDUNCULATE BARNACLE *OCTOLASMIS MÜLLERI* (COKER, 1902) REARED IN THE LABORATORY[1]

WILLIAM H. LANG

Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Columbia, South Carolina 29208

Octolasmis mülleri (Coker, 1902) is a small pedunculate barnacle found attached to the gills of the blue crab, *Callinectes sapidus* and other decapod hosts (Walker, 1974). First described from Beaufort, North Carolina, by Coker (1902), *O. mülleri* is perhaps synonymous to the cosmopolitan *Octolasmis lowei* (Nilsson-Cantell, 1927; Causey, 1961) or a local race or subspecies (Pilsbry, 1953) of a shallow-water *O. lowei*-series (Newman, 1967). In the western Atlantic its known range extends southward from the Chesapeake Bay (Van Engel, 1972) through the Gulf of Mexico and Caribbean Sea to Brazil (Lacombe, personal communication). Although Coker (1902) noted an increase in barnacle numbers in late summer, the breeding season is unknown.

The complete larval deveolpment for this species or other members of the family Poecilasmatidae has not been described. The first and second naupliar stages and cyprid of *O. mülleri* were described by Coker (1902) but attempts to rear larvae failed. Of the pedunculate barnacles in general, complete larval descriptions exist only for *Scalpellum scalpellum* L. (Kaufmann, 1965), *Pollicipes mitella* L. (Yasugi, 1937), *Pollicipes spinosus* Quoy and Gamard (Batham, 1945b), *Pollicipes polymerus* Sowerby (Lewis, 1975), *Ibla idiotica* Batham (Batham, 1945a), *Ibla quadrivalvis* Cuv. (Anderson, 1965), *Lepas fascicularis* Ellis and Solander (Willemos-Suhm, 1876; Bainbridge and Roskell, 1966) and *Lepas pectinata* L. and *Lepas anatifera* Spengler (Moyse, personal communication).

The present study was undertaken to determine the breeding season of *O. mülleri* in a South Carolina estuary, to describe the life stages of the species through laboratory rearing and to establish criteria for staging of larvae in future experiments.

Methods

Using wire mesh crab pots, blue crabs were collected at two to four week intervals at North Inlet, South Carolina from June 1974 to October 1975. Crab gills were examined for *O. mülleri*, the total number of barnacles and the number gravid (egg mass visible in the mantle cavity) being noted. During the summer and fall (July–November), gravid barnacles were teased off the gills and isolated in 35‰ sea water at room temperature (24–29° C).

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Released stage I nauplii were placed in fresh sea water and following molting to stage II, larvae were transferred to 8 cm Carolina culture dishes, 50–100 larvae per dish. For determination of development time, active larvae were transferred to 5.5 cm dishes, five larvae per dish. The algae *Monochrysis* sp., *Isochrysis galbana, Pseudoisochrysis paradoxa, Tetraselmis suecia,* or *Dunaliella tertiolecta* were added to individual cultures. Plant cells and sea water were changed at two-day intervals. Based on original results, fifteen additional larvae were reared on a mixture of *Monochrysis* and *Tetraselmis,* five larvae per 5.5 cm dish. All cultures were maintained at 30‰ and room temperature.

Dead larvae and exuviae were preserved in 70% ethanol. Drawings were made from freshly sacrificed larvae slightly flattened by coverslip pressure using camera lucida. Measurements were made with an ocular micrometer on unflattened preserved larvae. Total length was measured from the mid-anterior carapace edge to the dorsal spine tip. Carapace width was measured at the widest part of the carapace. Carapace length (stages, V, VI) was measured from the mid-anterior to mid-posterior carapace edges.

Some aspects of the external morphology of settlement and metamorphosis of *O. mülleri* larvae were observed by exposing a newly molted blue crab to ten reared cyprid larvae. The crab gills were examined 16 hours later and gill platelets with attached larvae were removed and placed in 35‰ sea water.

Results

O. mülleri were present on blue crabs every month from June 1974 to October 1975. Incidence on crabs was variable and is presently being studied in detail. Gravid barnacles were noted every month, the percent of gravid individuals varying from below 10% during February–March to above 40% during August–November. Cyprid larvae (attached to the gills), were found during July–October. Up to 70 larvae were found per crab, incidence being greatest in September and early October.

Larvae reared in the laboratory pass through six free-swimming naupliar stages and one cyprid stage. In the small cultures, *Dunaliella* produced 100% mortality of barnacle larvae within two days. All other algal species supported some larvae development: *Tetraselmis,* stage III; *Pseudoisochrysis,* stage III; *Isochrysis,* stage V; and *Monochrysis,* stage VI. Only the mixture of *Monochrysis* and

Table I

Mortality (%) and earliest day of molt for each stage of reared larvae of Octolasmis mülleri.

Food	Stage II initial number	II		III		IV		V		VI		Cyprid	
		%	day	%	day	%	day	%	day	%	day	%	day
Monochrysis	30	17	1	32	6	41	10	40	14	100	18	—	—
Monochrysis / Tetraselmis	15	0	1	0	4	0	6	0	7	0	9	7	15

Tetraselmis allowed complete development to cyprid (Table I). For *Monochrysis*, stage VI larvae developed in 18–22 days; for *Monochrysis/Tetraselmis*, larvae developed in 9–10 days. In the latter culture, development time to cyprid ranged from 14 to 18 days.

Larvae in the large cultures became tangled in clumps of three to ten individuals, resulting in substantial initial mortality. Otherwise the effects of different algae species were similar to small culture results.

Larvae

The most significant characters for naupliar and cyprid stages follow.

Stage I. (Fig. 1, I). Accurately described by Coker (1902), this stage is characterized by curved frontolateral horns projecting caudolaterally and short undeveloped caudal spine and abdominal process. Molting to stage II begins almost immediately after release from the mantle cavity.

Stage II. (Fig. 1, II). Present findings vary somewhat on setule arrangements indicated by Coker (1902) (Fig. 2). The nauplius assumes a form distinct from reported balanomorph larvae. A long barbed caudal spine and a shorter barbed abdominal process are present. No distinct lateral spines exist on the carapace. Frontal filaments are present in this and all subsequent naupliar stages.

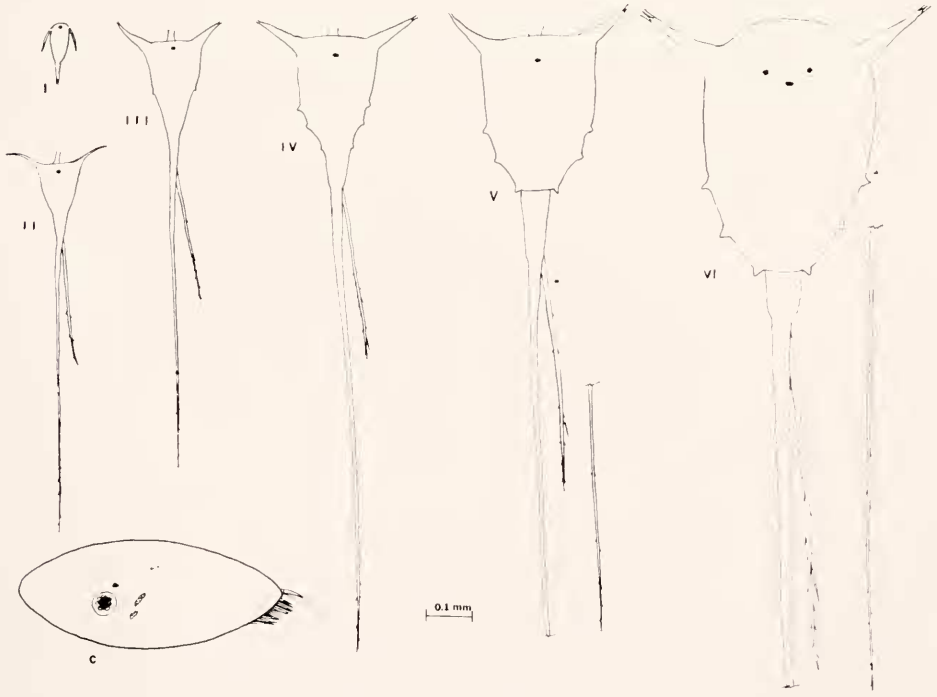

FIGURE 1. Carapace outlines of the six naupliar stages (I–VI) and cyprid (C) of *Octolasmis mülleri*.

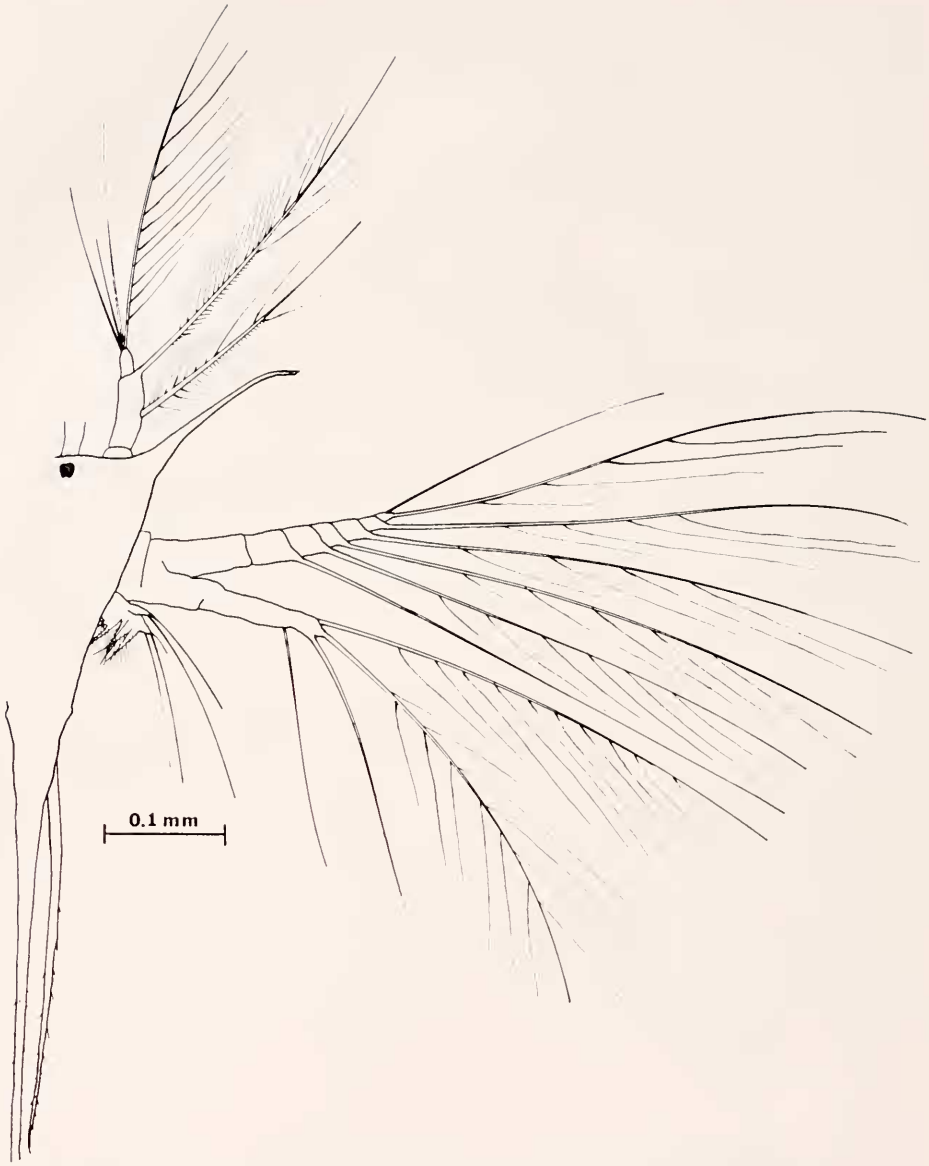

FIGURE 2. Dorsal view of the stage II naupli of *Octolasmis mülleri* showing complete setation of appendages.

The frontolateral horns project forward and have a plain tip (Fig. 3A). The single-lobed labrum tapers to a small rounded tip, the form remaining constant in all stages (Fig. 4). Setae line the distal portion.

Stage III. (Fig. 1, III). The frontolateral horn tip is trifurcate with tufts of fine setae and one minute setose seta extending from the central core. Apparently

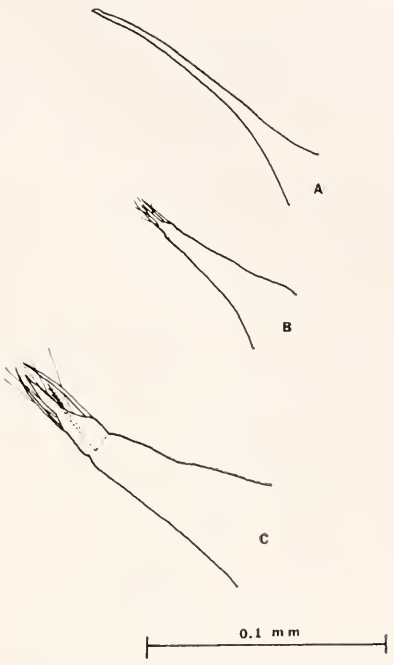

FIGURE 3. Ventral view of the frontolateral horns of stage II (A), stage III (B) and stage VI (C) nauplii. The number of fine setae has been reduced for graphic clarity.

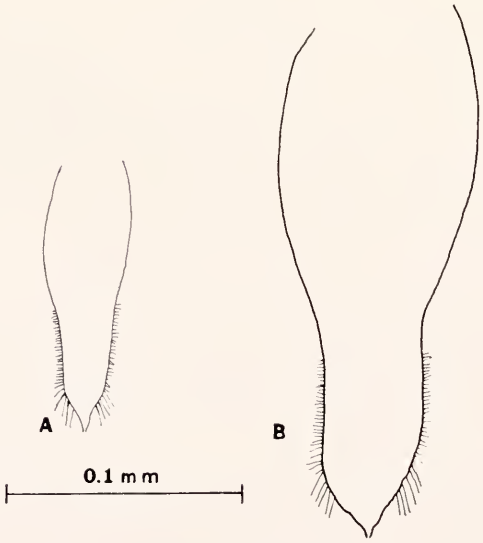

FIGURE 4. Ventral view of the labrum of stage II (A) and stage VI (B) nauplii.

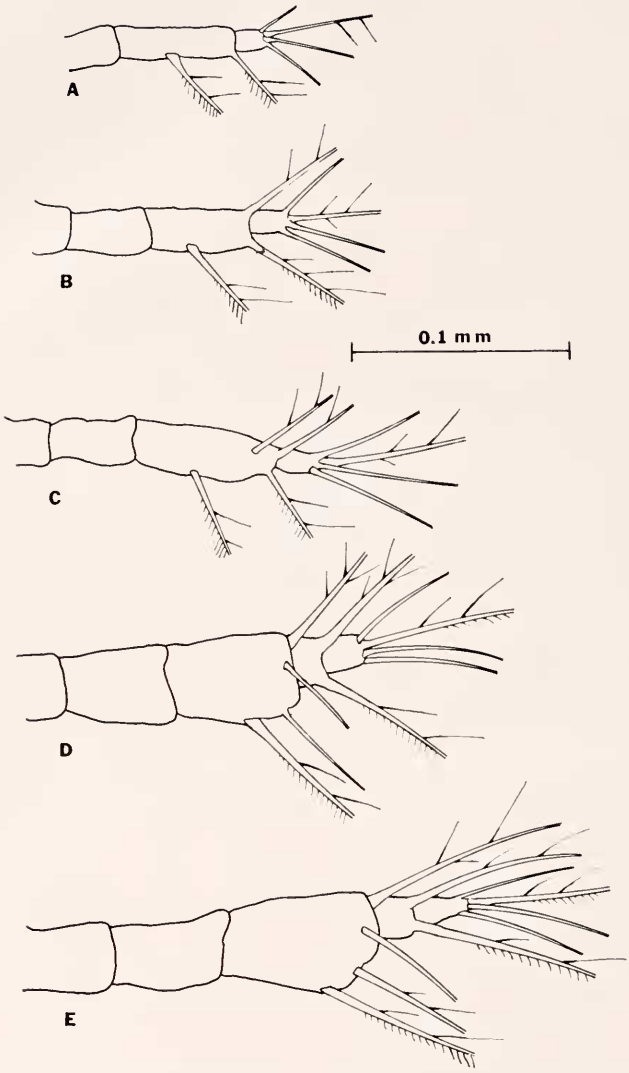

FIGURE 5. Antennules of stage II (A), stage III (B), stage IV (C), stage V (D) and stage VI (E) nauplii. A series of short lines indicates a bristled shaft (see text).

sensory in nature, this structure is present in stages III–VI (Fig. 3). One pair of lateral spines is distinct on the carapace. A pre-axial seta is found on the antenna (Fig. 6B).

Stage IV. (Fig. 1, IV). The carapace bears three pairs of lateral spines. The abdominal process has one distinct spine at its dorsal portion.

Stage V. (Fig. 1, V). The posterior border of the carapace is clearly defined and the lateral spines are proportionally larger. A swelling of the antennule third segment is evident (Fig. 6D).

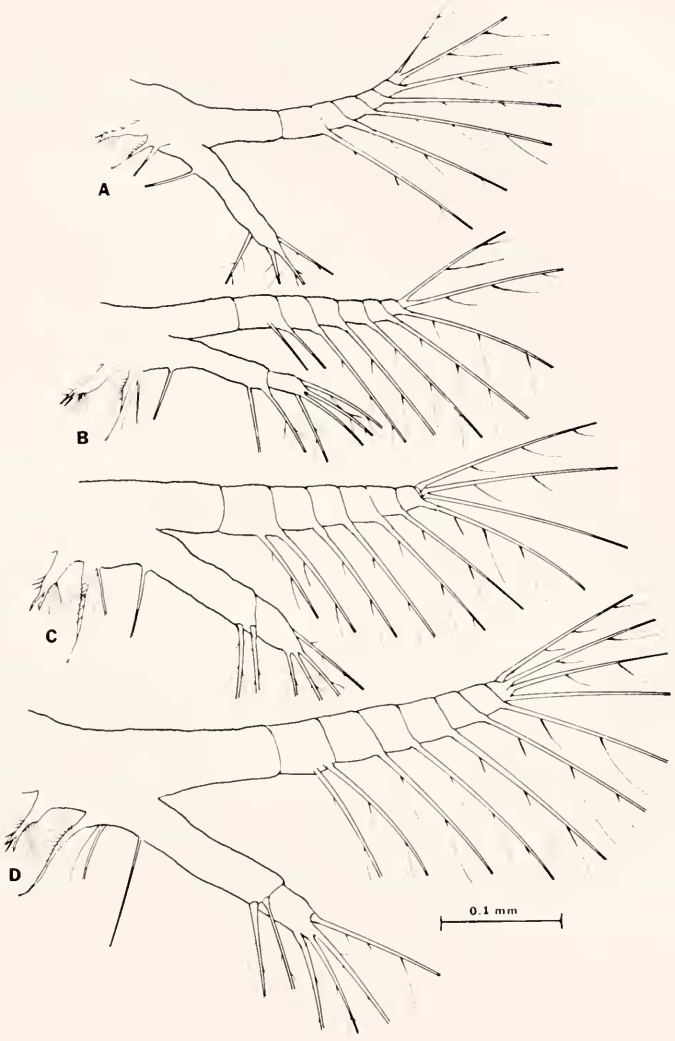

FIGURE 6. Antennae of stage III (A), stage IV (B), stage V (C) and stage VI (D) nauplii.

Stage VI. (Fig. 1, VI). The carapace broadens to an oval shape, obscuring dorsally the mandibles and frontal filaments. No paired eyespots are evident initially but become distinct within two to three days. Thoracic limb outlines are visible through the cuticle.

Cyprid. (Fig. 1, C). The carapace form is typical of most described cyprid larvae. In live specimens the cyprid is transparent with an amber tinge. A distinct orange pigmented area is present slightly posterior to the paired eyes.

Setation becomes more elaborate with successive molts (Figs. 5–7). Relative to balanid larval appendages, the antennule and antenna of *O. mülleri* nauplii are

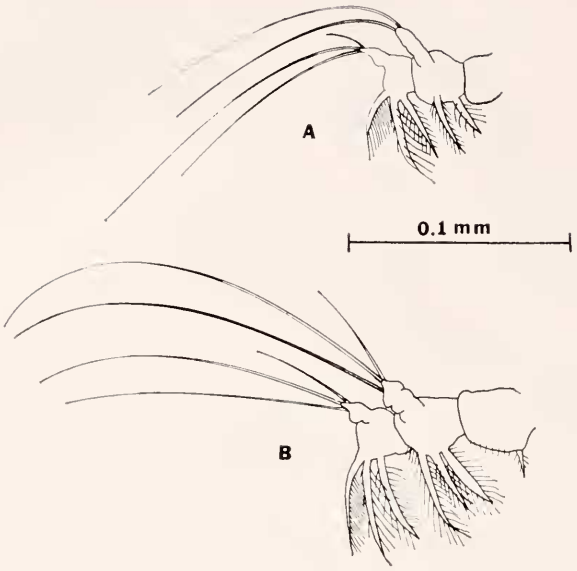

FIGURE 7. Mandibles of stage II (A) and stage V (B) nauplii.

elongate while the mandible is small with a very simple and indistinctly segmented exopodite (Fig. 7). Setae and setules are generally long and very delicate. Rather than the typical arrangement of hairlike setules coming off opposite sides of the setal shaft, the plumose setae of *O. mülleri* often have setules concentrated on one side of the shaft. This is particularly evident on the antennal exopodite. The antennule bears one (stage II) to three (stages IV–VI) setae with relatively thick shafts lined with short bristle-like setules and numerous closely spaced long setules (Fig. 2). These appear to serve as fine filtering devices. The setation formula of Newman (1965) as modified by Sandison (1967) is given in Table II. No major variations in setation were observed in this study.

The triangular carapace is smooth and transparent with no dorsal spines. A distinct pair of marginal spines first appears at stage III. These increase to three

TABLE II

Setation formula for nauplii of Octolasmis mülleri.

Stage	Antennule	Antenna		Mandible	
		Exopodite	Endopodite	Exopodite	Endopodite
6	P P SPSS P S P P	3PS 7P	4P 2P S SSC G	3S 3S	CPP PPP G
5	P P SPSS P S S P	2PS 7P	4P 2P S SSC G	3S 3S	CPP PPP G
4	P P SPSS P P	2P 5P2S	3PSPS S SSC G	2S 3S	CPP PPP G
3	P SPSS P P	2P 5P	3P P S S C G	2S 3S	CPP PPP G
2	SPSS P P	SP 4PS	2PSS S S C G	2S 3S	CPP PP
1	SSSS S S	SS SSS	3S S S G	2S 2S	SSS SS

TABLE III

Measurements of larval stages of Octolasmis mülleri *reared under laboratory conditions.*

Stage	Number measured	Carapace				Total length (mm)	
		Width (mm)		Length (mm)			
		Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$
II	8	(0.10–0.11)	0.107	—	—	(0.79–0.85)	0.814
III	10	(0.12–0.14)	0.125	—	—	(0.92–1.11)	1.004
IV	9	(0.16–0.18)	0.173	—	—	(1.18–1.34)	1.270
V	6	(0.23–0.27)	0.247	(0.32–0.36)	0.343	(1.67–1.82)	1.735
VI	9	(0.36–0.39)	0.378	(0.52–0.55)	0.535	(2.54–2.78)	2.659
cyprid-reared	10	(0.21–0.26)	0.223	(0.54–0.59)	0.572	—	—
cyprid-"wild"	4	(0.21–0.23)	0.222	(0.54–0.57)	0.567	—	—

pairs at stage IV. A well-defined posterior carapace border develops only after the fourth molt. The marginal spines are often less developed on one side relative to the other and at times one or more will be missing entirely. The carapace size remains relatively constant per stage with a distinct size increase at each molt (Table III).

Reared cyprids were uniform in shape and nearly identical to "wild" specimens in both size (Table III) and pigmentation. A distinct orange pigment is usually restricted to one or two compact areas between the compound eyes and natatory appendages. The color remains evident through metamorphosis and perhaps is similar to the yellow cells of *Balanus balanoides* cyprids (Walley, 1969). The bright orange pigment however is distinct from any coloration observed in cyprids of *Balanus eburneus* and *Chelonibia patula* reared in this laboratory.

A sequence of abdominal spines similar to that of Balanidae (Moyse, 1961) or *Lepas fascicularis* (Bainbridge and Roskel, 1966) does not occur in *O. mülleri*. A paired row of small spines is sometimes seen on the abdominal process of stage II nauplii (Coker, 1902) but is not evident in later stages. The abdominal process is covered with numerous spinules and in stages IV–VI has a single spine near its distal end. The lesser barbed caudal spine is longer than the abdominal process in all stages.

The tapered single-lobed labrum of *O. mülleri* is distinct from the broad, flat-edged labrums of *Lepas fascicularis* (Bainbridge and Roskell, 1966) or *Pollicipes mitella* (Yasugi, 1937) and *Pollicipes polymerus* (Lewis, 1975). This form may be characteristic for the genus but comparative descriptions are needed.

Cyprids introduced to a newly molted blue crab were rapidly drawn into the gill chamber. Of ten initial larvae, six were found attached to the gills 16 hours later. The exact times of attachment are unknown but in each both antennules of the cyprid were cemented to a single gill platelet (Fig. 8A). After removal from the gill, four cyprids continued metamorphosis to adults. At initial recovery the peduncle outline was visible through the cyprid carapace (Fig. 8A). The capitulum outline became progressively more distinct while internal areas turned

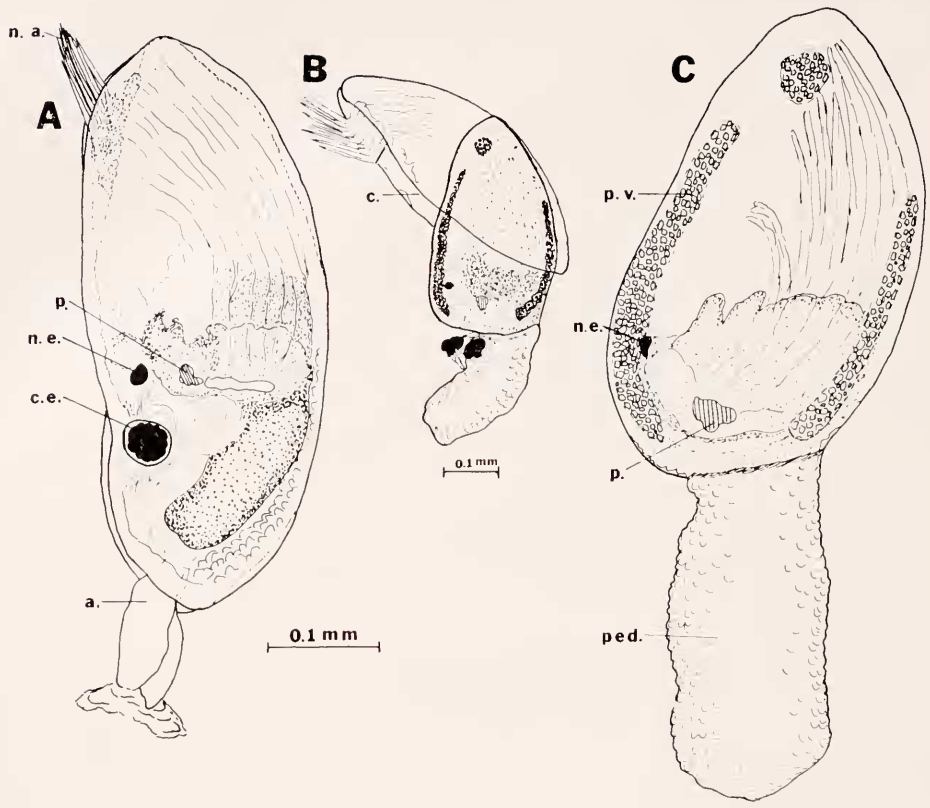

FIGURE 8. A. Cyprid of *Octolasmis müllcri* recovered from blue crab gill 16 hours after exposure. Prominent features include the cemented antennules (a.), compound eye (c.e.), natatory appendages (n.a.), nauplius eye (n.e.) and orange pigment spot (p.). B. By 36 hours after recovery the cyprid carapace (c.) is nearly shed. C. The newly emerged juvenile barnacle still retains the nauplius eye (n.e.) and pigment spot (p.). Primordial valves (p.v.) and expanded peduncle (ped.) are evident.

opaque. From 20 to 72 hours post-recovery, the carapace, natatory appendage exuvium and compound eyes were shed (Fig. 8B). The newly emerged adults exhibited stalk movement and slight cirral and valve movement. The naupliar eye and orange pigment were still visible and the five primordial valves evident (Fig. 8C). The orange pigment appears closely associated with the gut region.

Young adults exhibit little activity at first but between two to three days after metamorphosis a full extension of the cirri was noted. At this point the orange pigment has disappeared and the naupliar eye is indistinct. The young barnacles will readily feed on crushed *Artemia*.

DISCUSSION

Field results indicate that breeding of *O. müllcri* and cyprid settlement on crabs is restricted to summer and fall months. Although adults are often maintained in

this laboratory at 10° C without apparent ill effects, release of larvae rarely occurs below 15° C and initial attempts to rear larvae at 15° C have failed. At this temperature the swimming motion of the larvae is slow and unsteady. Feeding is probably greatly reduced or impossible. The northern extension of *O. mülleri* appears to be limited by the temperature requirements for breeding and larvae development. The exact temperature requirements need to be established.

In most cases larval development of barnacles proceeds through six free-swimming naupliar stages and one cyprid stage prior to settlement and metamorphosis to the adult form (Newman, Zullo and Withers, 1969). Normally the stage I nauplius is nonfeeding and rapidly molts, while stages II–VI are actively feeding larvae filtering plankton. Several lecithotrophic larvae will develop without feeding (Batham, 1945a, 1945b; Anderson, 1965; Kaufman, 1965). *O. mülleri* nauplii swim dorsal side up directing fine particles toward the labrum by sweeping motions of their appendages. They appear to effectively filter dilute algal suspension and rapidly become fouled in dense cultures.

In laboratory cultures the development time of *O. mülleri* from newly-hatched egg to cyprid is 14–18 days at 24–29° C. This compares favorably with development times for local balanid species reared in the laboratory: *Balanus eburneus*, 7–12 days at 26° C (Costlow and Bookhout, 1957), *Balanus amphitrite denticulata*, 7–10 days at 26° C (Costlow and Bookhout, 1958) and *Balanus galeatus*, 9–14 days at 23–25° C (Molenock and Gomez, 1972). Extremes in development times of planktotrophic nauplii range from 22 hours for *Chthamalus stellatus stellatus* at an unspecified temperature (Daniel, 1958) to 57 days for *Lepas anatifera* at 20° C ± 3° C (Moyse, 1963). The extraordinary time cited by Daniel needs verification; however, monthly plankton samples in the North Atlantic support the findings of Moyse of a long larval life for *Lepas anatifera* (Bainbridge and Roskell, 1966). Although stage II *Lepas* larvae, ranging in length from 0.6 to 0.8 mm (Groom, 1894), are nearly equal in length to stage II *O. mülleri*, *Lepas* larvae are over 9 mm by stage VI (Moyse and Knight-Jones, 1967; Bainbridge and Roskell, 1966). *O. mülleri* has neither a long larval life nor exceptional growth increments.

Of the few barnacle nauplii described, *O. mülleri* most closely resembles the lepad larvae. The very long caudal spine and abdominal process are characteristic of both groups, as are relatively long setae and setules and long tufted frontolateral horns (Willemoes-Suhm, 1876). The difference in general appearance between these larvae and the short compact balanid larvae is striking, but is merely a result of proportional size differences in common structures.

O. mülleri larvae exhibit a curious underdevelopment of certain posterior features relative to other barnacle larvae. The mandibles remain small and show little change with successive molts, the exopodite, in particular, being greatly reduced. The mandibular gnathobase is also reduced, suggesting a possible modified feeding pattern. A rudimentary maxillule, a common feature of later stage nauplii (Bassindale, 1936; Bainbridge and Roskell, 1966), is absent as are the lateral paired abdominal spines previously mentioned. A clearly-defined posterior carapace border has been a consistant feature of stage IV larvae (Jones and Crisp, 1954; Barnes and Costlow, 1961) but is delayed until stage V in *O. mülleri*. The significance of this trend is unknown.

Settlement of *O. mülleri* appears to be highly specific for decapod gills. Reared cyprids do not settle on culture dish surfaces or excised crab gills but will settle on gills of live crabs. Metamorphosis has been observed in four individuals, but a means for continuous observation of settlement has not yet been devised. Metamorphosis of *Octolasmis* appears similar to *Lepas* (Newman *et al.*, 1969). The five primordial valves are distinct before the cypris carapace is shed but, unlike *Lepas,* the valves are separated by large interspaces. Further details on subsequent valve calcification in juvenile forms is now under investigation.

This paper is based on part of a dissertation to be presented to the faculty of the Marine Science Program, University of South Carolina, in partial fulfillment for the Doctor of Philosophy Degree. I wish to thank Dr. W. B. Vernberg, Dr. B. C. Coull, and Dr. P. A. Sandifer for reading and criticizing the manuscript and Mr. J. Takahashi for his initial help in maintaining the algae used for this project.

Summary

1. The larval phase of *O. mülleri* consists of six naupliar stages and one cyprid stage. Descriptions and distinguishing characteristics are given for each stage.

2. Based on field observations and initial laboratory results, the breeding season of *O. mülleri* is probably restricted to summer months in temperate regions. Larvae appear unable to effectively feed at 15° C or below.

3. In small cultures, 93% of the larvae reached the cyprid stage using a mixed algae diet of *Tetraselmis suecia* and *Monochrysis* sp.

4. Larval development from newly-hatched nauplii to cyprid ranges from 14 to 18 days at room temperature (24–29° C) in laboratory culture.

5. Larvae most closely resemble described lepad larvae in general body form but have reduced mandibles and lack a series of abdominal spines reported for both balanid and lepad nauplii. The development of a posterior carapace border is delayed until stage V.

6. Reared cyprids were identical to "wild" specimens in morphology and size. Settlement of cyprid stages occurred only on live crabs. Some aspects of the external morphology of metamorphosis are described.

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